Ammonoid Locomotion

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Abstract: Because ammonoids have never been observed swimming, there is no alternative to seeking indirect indications of the locomotory abilities of ammonoids. This approach is based on actualistic comparisons with the closest relatives of ammonoids, the Coleoidea and the Nautilida, and on the geometrical and physical properties of the shell. Anatomical comparison yields information on the locomotor muscular systems and organs as well as possible modes of propulsion while the shape and physics of ammonoid shells provide information on buoyancy, shell orientation, drag, added mass, cost of transportation and thus on limits of acceleration and swimming speed. On these grounds, we conclude that ammonoid swimming is comparable to that of Recent nautilids and sepiids in terms of speed and energy consumption, although some ammonoids might have been slower swimmers than nautilids.

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Chapter 17
Ammonoid Locomotion

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17.1 Introduction

The locomotor capacity of ammonoids is still a matter of much debate. This question is intimately linked with questions concerning ammonoid habitat and buoyancy (Ritterbush et al. 2014). Aspects of buoyancy were reviewed by Hoffmann et al. (2015). Based on theoretical models of ammonoid buoyancy (e.g., Trueman 1941; Saunders and Shapiro 1986) in combination with the latest empirical studies on volume models of ammonoids (Tajika et al. 2015; Naglik et al. 2015), we can now confidently reject the hypothesis of an obligatorily benthic mode of life for most ammonoids advocated by Ebel 1983 (see also Westermann 1993, 1996; Kröger 2001 or Jacobs and Chamberlain 1996 for views contrasting Ebel's ideas). The function of the phragmocone as a buoyancy device has been corroborated by a great number of studies (see Hoffmann et al. 2015 and references therein) including the latest volume models of ammonoid shells and the linked buoyancy calculations (Tajika et al. 2015; Naglik et al. 2015), most mathematical models of buoyancy (Hoffmann et al. 2015), the convergent evolution of an upward orientation of the aperture in many

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major ammonoid lineages (e.g., Raup and Chamberlain 1967; Bayer and McGhee 1984; Saunders and Shapiro 1986; Klug 2001; Korn and Klug 2003; Monnet et al. 2011) and the increase of phragmocone complexity through ammonoid evolution (Saunders 1995; Saunders and Work 1996, 1997; Daniel et al. 1997; Saunders et al. 1999). This is significant because *syn vivo* shell orientation can be used as an indicator of locomotion and habitat preference, although there are great limits for the accuracy of such conclusions.

Several authors have sought information on habitat depth and swimming speed in the physical properties of ammonoid shells. For example, shell implosion depths suggest limits for maximum diving depths (e.g., Westermann 1973, 1996; Saunders and Wehman 1977; Jacobs 1992a; Hewitt 1996; Batt 2007). Inferences on diving depth and ammonoid behavior have also been drawn based on siphuncle properties (e.g., Westermann 1971, 1996; Mutvei and Reyment 1973; Mutvei 1975; Chamberlain and Moore 1982; Ward 1982; Hewitt 1996). Oxygen isotopes have also been used to approximate diving/living depths of ammonoids (Moriya et al. 2003; Lukeneder et al. 2010, Lukeneder 2015; Moriya 2015).

Similarly, streamlining and drag have been quantified for a wide range of shell shapes (Kummel and Lloyd 1955; Westermann 1971, 1996; Reyment 1973; Chamberlain 1976, 1981; Chamberlain and Westermann 1976; Jacobs 1992b, Jacobs et al. 1994; Monnet et al. 2011; Ritterbush and Bottjer 2012; Ritterbush et al. 2014), and the results related to mode of life. Mutvei and Reyment (1973) as well as Mutvei (1975) argued that muscle attachment was too small and weak to allow ammonoids to swim well. However, there is some indication suggesting that ammonoids may have powered their locomotion with a muscular mantle not firmly attached to the shell (Jacobs and Landman 1993; Jacobs and Chamberlain 1996). Muscle attachment is discussed in detail in Doguzhaeva and Mapes (2015).

Sedimentary facies in which ammonoids are preserved may provide some information about lifestyle and habitat (Wang and Westermann 1993; Westermann 1996; Tsujita and Westermann 1998; Westermann and Tsujita 1999), although post mortem transport can complicate the picture (e.g., Kennedy and Cobban 1976; Tanabe 1979: Westermann 1996 and references therein). Nevertheless, the broad range of facies types in which ammonoid remains occur in combination with the great disparity in shell morphology supports a wide variety of life habitats and habits for these animals that in principle relate to differing locomotor capabilities as exemplified by Jacobs et al (1994).

Another line of evidence comes from sublethal injuries. It was especially Keupp (review in Keupp and Hoffmann 2015), who, in a series of articles (Keupp 1984, 1985, 1992, 1996, 1997, 2000, 2006, 2008, 2012), proposed that several types of injuries commonly recorded in ammonoid shells were inflicted by benthic crustaceans. If that is correct, this would support at least a temporarily demersal habitat for ammonoids showing such injuries; other injuries related to nektic predators, however, corroborate a nektic mode of life for at least some ammonoid groups (compare Ritterbush et al. 2014; Keupp and Hoffmann 2015).

Finally, *syn vivo* epizoans also provide some information on swimming direction and orientation of the shell (Keupp et al. 1999). However, such cases of epizoans

that can be interpreted in that respect are rare (Seilacher 1960, 1982a, b; Keupp et al. 1999; Seilacher and Keupp 2000; Hauschke et al. 2011). De Baets et al. (2015b) review information obtained from epizoans attached to ammonoids as a function of orientation (e.g., Seilacher 1960). Their results support the swimming orientations discussed herein.

Because ammonoids apparently did not produce unequivocal trace fossils of their movements *syn vivo*, no evidence from this source is available to help interpret ammonoid locomotion.

17.2 Limits of Research on Ammonoid Locomotion

Because ammonoids are extinct, we cannot provide direct, observational evidence on their swimming ability from study of the living creatures. There is no direct way to measure such parameters as maximal swimming speed, maneuverability, or the efficiency of the musculature in extinct animals like ammonoids. Thus, in this paper we attempt to reconstruct ammonoid swimming ability and maneuverability using indirect evidence that can be gleaned from the fossil record; from analogy to the performance of modern relatives; and from awareness of the uncertainties inherent in such an effort.

There are only a few aspects of ammonoid locomotion, which at the outset appear highly plausible to us:

1. Ammonoids generally were able to produce neutral buoyancy by means of their buoyancy apparatus.
2. Most ammonoids were not fully benthic since they did not leave any traces in the sediment, had often upward pointing apertures and were preyed upon by nektic organisms or only from below by benthic organisms.
3. Most ammonoids were probably capable of swimming movement powered by jet propulsion, arm beating, or other mode of propulsion.
4. Locomotor capabilities were not uniform across all ammonoid taxa since they had sometimes quite large differences in shell orientation, hyponomic sinus, body size or shell shape.

17.3 Shell Orientation

17.3.1 Mathematical Models

With his pioneering work on ammonoid shell geometry and buoyancy, Trueman (1941) initiated a line of investigation that continues down to the present day, in which palaeontologists utilize mathematical modeling techniques to gain insight on ammonoid buoyancy and shell orientation. These models usually employ the parameters used by Raup and Chamberlain (1967), namely W (expansion rate), K

(area of last generating curve) and R (distance from the coiling axis). However, such models are predicated on a number of simplifications (e.g., Trueman 1941; Raup (1967); Raup and Chamberlain (1967); Ebel 1983; Saunders and Shapiro 1986; Shapiro and Saunders 1987; Okamoto 1988, 1996; Klug 2001; Korn and Klug 2003). Commonly, these models include the assumption of self-similar (gnomonic), logarithmic shell growth, uniform shell thickness independent of position on the whorl section and the presence of a stable coiling axis. None of these simplifying assumptions necessarily coincide with actual ammonoid shells, i.e., shell growth in ammonoids was not perfectly logarithmic (e.g., Okamoto 1996; Klug 2001; Korn 2012; Tajika et al. 2015; Naglik et al. 2015), shell thickness varies and the coiling axis can permanently change its position throughout ontogeny (e.g., Urdy et al. 2010a, b).

Most authors, who produced mathematical models of shell geometry (Trueman 1941; Raup 1967; Raup and Chamberlain 1967; Saunders and Shapiro 1986; Okamoto 1988, 1996), tested their models, usually with data from Recent nautilids (Packard et al. 1980; Chamberlain 1987; Ward 1987; Jacobs and Landman 1993), and found reasonably good agreement between their results and the modeled attributes of the living animal. According to these models, the orientation of the aperture largely depended on the whorl expansion rate and ranged between about 30° and 110° from the vertical direction in normally coiled ammonoids with planispiral shells (Saunders and Shapiro 1986). In straight bactritoids (Fig. 17.1) and other heteromorph ammonoids, the aperture may have faced more or less downward, for example in more or less orthoconic forms (without counterbalancing options) such as baculitids or in some early ammonoids with very loosely coiled shells such as *Metabactrites* (e.g. Klug and Korn 2004), or in subadult *Anisoceras*, turrilitids and other heteromorphs. As shown in Fig. 17.1, shell orientation may have varied quite strongly throughout ontogeny.

As shown by Westermann (1996), the majority of Mesozoic ammonoids had body chamber lengths between 200° and 300° (Fig. 17.2). According to him and the model by Saunders and Shapiro (1986), this would coincide with an apertural orientation of about 80° to 100°, i.e. with the aperture oriented more or less horizontally. Only forms with extremely high or extremely low whorl expansion rates and body chambers shorter than half a whorl or exceeding one whorl in length would have had an aperture oriented below 50° from vertical.

17.3.2 Mechanical Models

In addition to mathematical modeling, some authors have employed mechanical, i.e. physical, models to help reconstruct shell orientation in ammonoids. Among the first to use such models were Mutvei and Reyment (1973), who built metal-coated, plastic shell models, vacuum molded from real ammonoid and *Nautilus* shells, to investigate the buoyancy and floating position of the animals thus modeled. These authors were later followed in using physical models by, e.g., Elmi (1991, 1993), Seki et al. (2000), Klug and Korn (2004), Westermann (2013) as well as Parent et al. (2014).

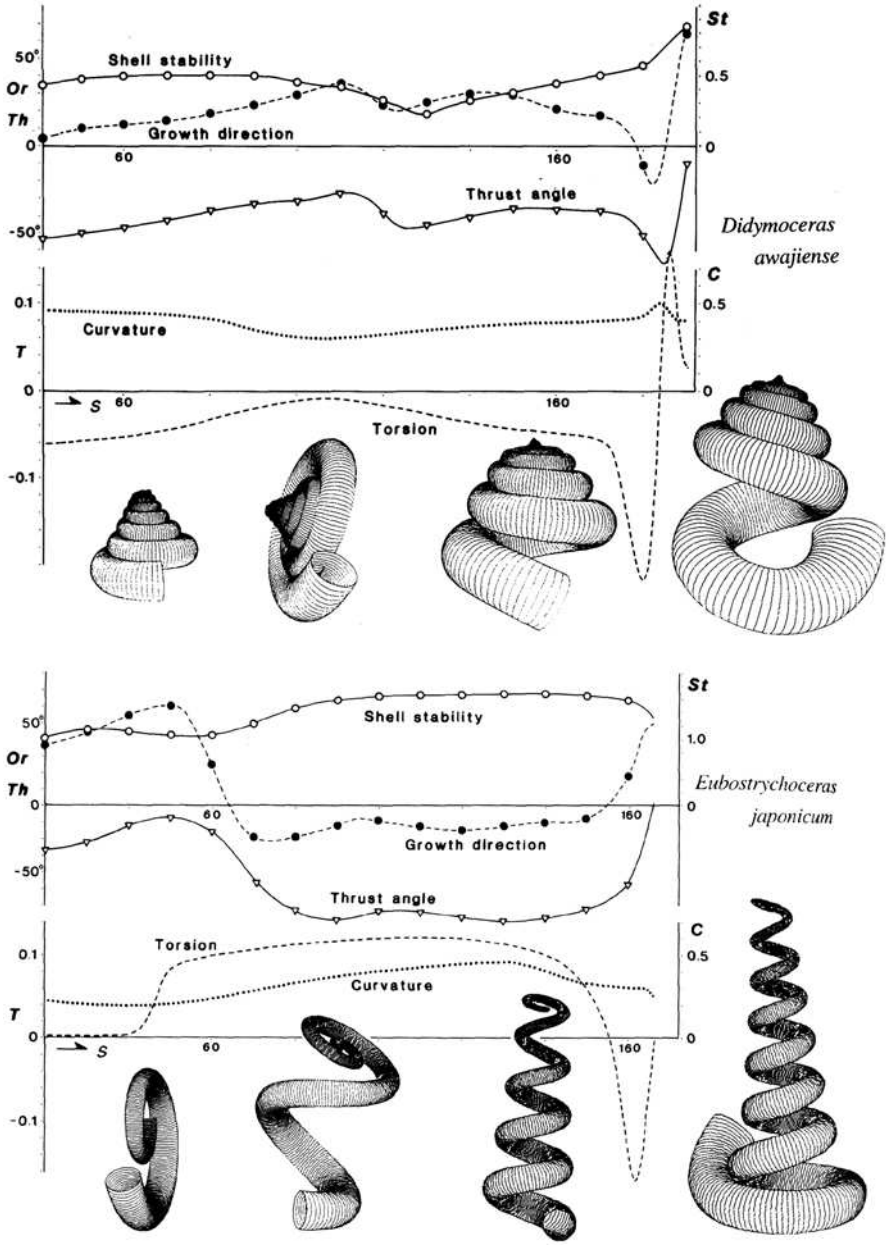

Fig. 17.1 Shell curvature, torsion, growth direction as well as hydrodynamic characters such as hydrodynamic stability, orientation of the aperture and hyponome jet thrust angle. (Source: Okamoto 1996)

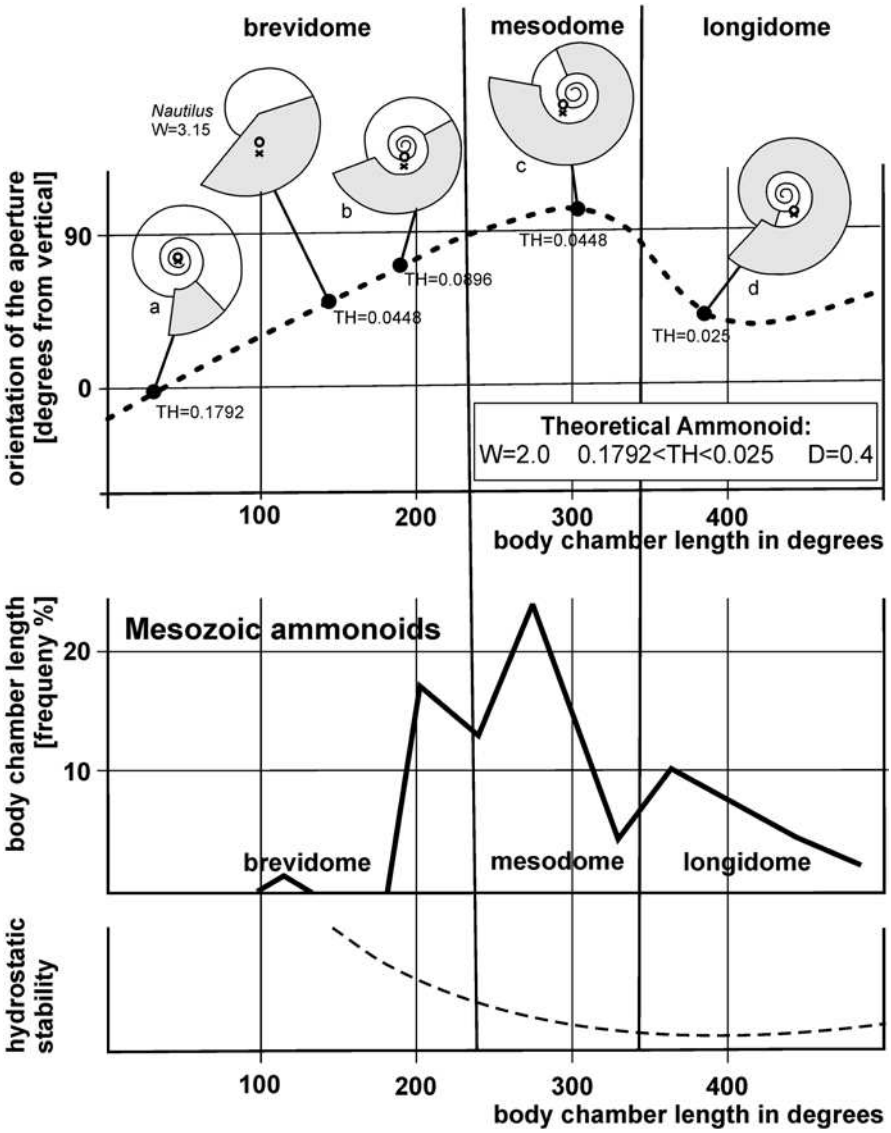

Fig. 17.2 Relationships between shell coiling, body chamber length, orientation of the aperture and hydrostatic stability of Mesozoic ammonoids. *W* whorl expansion rate, *TH* relative shell thickness, *D* relative distance between coiling axis and generating curve. Note the three peaks in body chamber length abundance and that these peaks coincide with a commonly sub-horizontal apertural margin and thus upward facing aperture. (Modified after Westermann (1996) incorporating a graph of Saunders and Shapiro (1986))

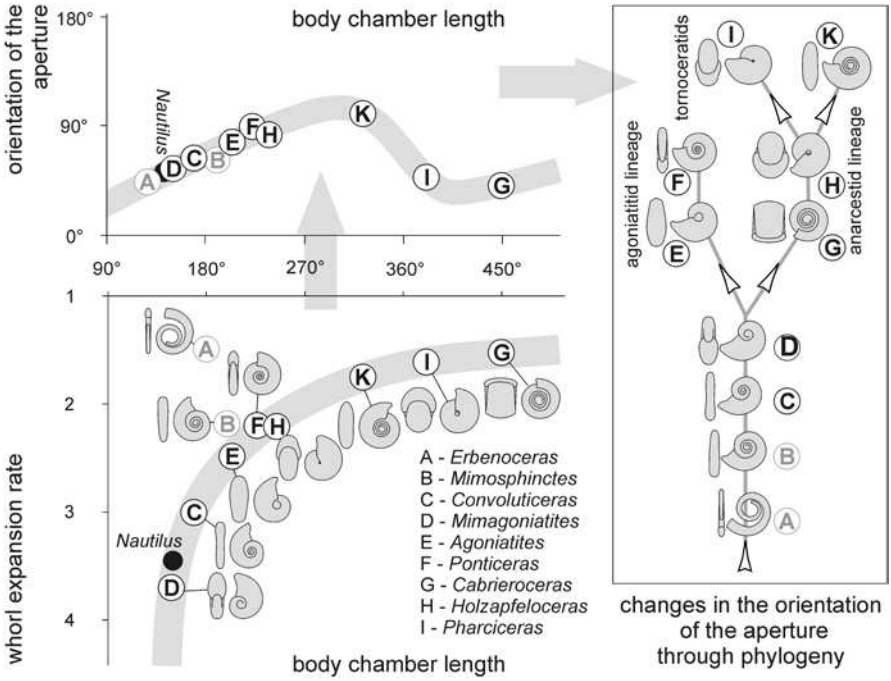

Fig. 17.3 Relationships between shell coiling, body chamber length, orientation of the aperture throughout the evolution of Devonian ammonoids. Note that three of the most important clades more or less independently evolved horizontal apertures early in the evolution of ammonoids. (Source: Klug and Korn 2004)

Klug and Korn (2004) showed, how shell orientation changed from facing downward in Orthocerida and Bactritida with orthoconic shells to oblique downward in Ammonoidea with loosely coiled shells, to oblique upward in less loosely coiled forms, to more or less horizontally upward in fully coiled shells (Fig. 17.3, 17.4). A progression of this type in aperture orientation is associated with iterative evolutionary trends (Fig. 17.3) in the major Devonian ammonoid clades (Mimosphinctoidea, Mimagoniatitoidea, Agoniatitoidea; Korn and Klug 2003) and even in parallel in two Devonian clades (Auguritidae and Pinacitidae; Monnet et al. 2011).

The question of whether ectocochleate cephalopods with orthoconic shells were capable of bringing their shell and body into a horizontal position is of long interest (e.g., Schmidt 1930; Ward 1976). Using physical models, Westermann (2013) demonstrated that a horizontal position in baculitid ammonoids could have been achieved by accumulating liquid in the most apical chambers. Such a horizontal position of cephalopods with orthoconic shells may also have been achieved with apical intracameral or intrasiphuncular deposits (e.g., Actinocerida, Endocerida) or chamber liquid (Westermann 1977, 2013; House 1981). For baculitids, Westermann (2013) suggested a vertical orientation of the shells of juveniles and a nearly horizontal orientation of subadults and adults because he assumed that juveniles had

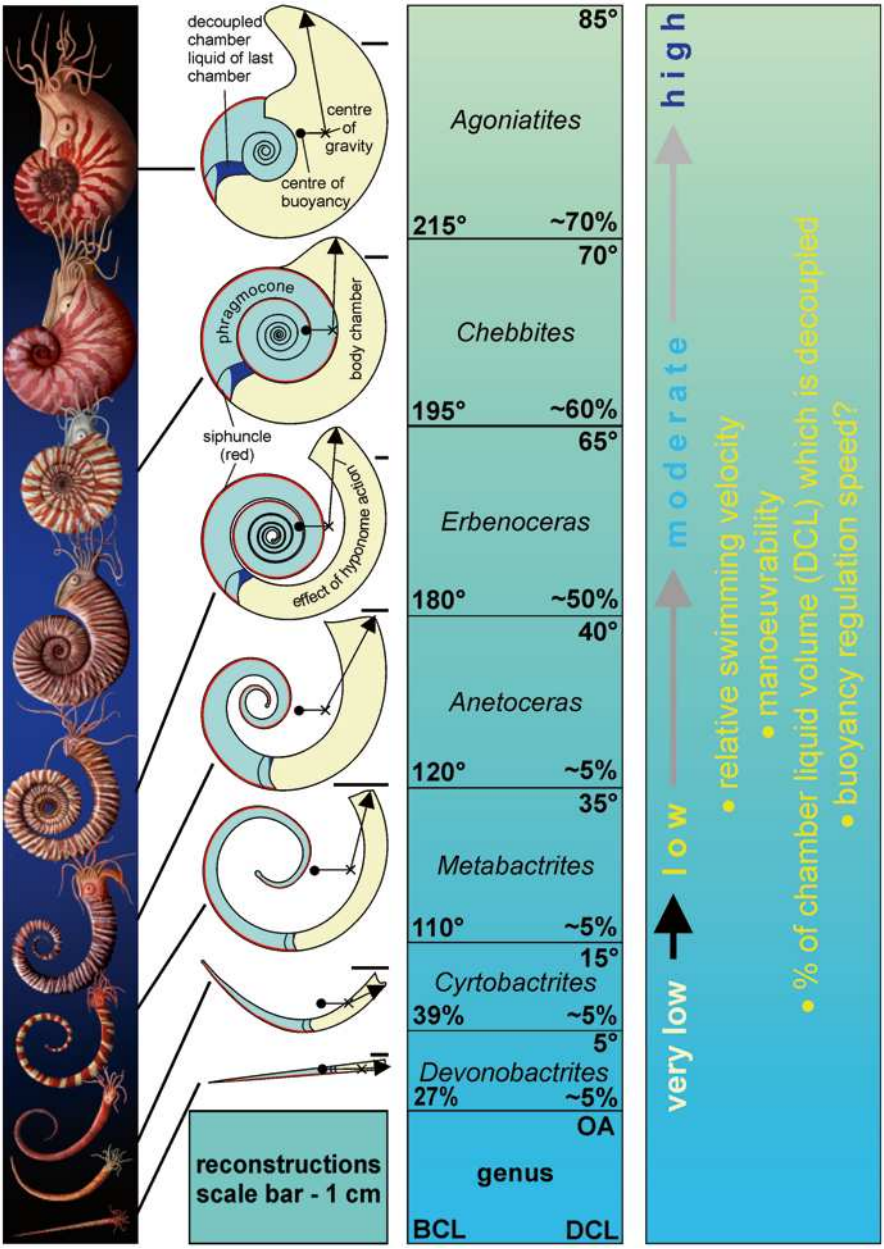

Fig. 17.4 Evolution of coiled ammonoid shells from straight bactritid shells and the consequences for body chamber length, aperture orientation, thrust angle of the hyponome jet, hydrodynamic stability and interpretations for swimming capabilities throughout evolution. (Modified after Klug and Korn 2004 as well as Klug et al. 2008). *BCL* body chamber length, *OA* orientation of the aperture, *DCL* decoupled chamber liquid.

phragmocones with more or less uniformly distributed liquid while in adults, the chamber liquid accumulated apically as a counterweight. The spatial distribution of chamber liquid might have also played a role in other ammonoids (Ward 1979, 1982; Kaplan 2002; Klug et al. 2008), although quantitative evidence on liquid distribution in ammonoid phragmocones has not yet been obtained.

Parent et al. (2014) experimented with a physical model comprised of weights and levers to assess the possible effect of the position of aptychi in aptychophoran ammonites on shell orientation. They concluded that in cases where the aptychus contains a sufficient mass and density relative to the animal's soft tissue and shell, the forward and backward movement of the buccal mass would have affected the orientation of the shell. Ammonites, such as some aspidoceratids, could have altered shell orientation in such a way that the aperture was lowered to < 25° from the vertical position.

Earlier physical models suggested capability of certain heteromorph ammonites (particularly the so-called "*shaft and hook shaped body chamber*" ammonoids; Kaplan 2002) to change their shell orientation (Kakabadzé and Sharikadzé 1993; Monks and Young 1998) by displacement of fluid and gas in the phragmocone (Kakabadzé and Sharikadzé 1993), or by moving the soft body of the animal within the living chamber, assuming that the animal was much smaller than its body chamber (Monks and Young 1998).

17.3.3 Empirical Models

We use the term "*empirical models*" to mean three-dimensional physical models of ammonoid shells constructed from stacks of cross-sections cut through a real shell. A similar approach was first employed by Chamberlain (1969), who built Plexiglas shell models from computer-produced topographic cross-sections of hypothetical ammonoid shells, which he then used for hydrodynamic experimentation (Chamberlain 1976, 1980, 1981). More recently, tomographic techniques have been developed, which greatly advance our skill to more confidently reconstruct *syn vivo* shell orientation(e.g., Longridge et al. 2009; Hoffmann and Zachow 2011; Hoffmann et al. 2013; Tajika et al. 2015; Naglik et al. 2015).These models are based on image stacks produced by different tomographic methods. Attempts to obtain image stacks by computer tomography often failed due to the lack of density contrast. This is probably the reason for the relatively late appearance of tomographic images of the interior of ammonoids in the scientific literature. Accordingly, tomographic data were sometimes obtained by serial sectioning (Tajika et al. 2015; Naglik et al. 2015). The latter method has the advantage that the images provide colour information and lack certain artifacts occurring in CT-data such as ring artifacts (see Hoffmann et al. 2013). In any case, these empirical models (Fig. 17.5) largely corroborate the results of mathematical modeling: forms with body chambers < 100° or > 360° have low apertures while the majority of shell forms with body chambers of 200° to 300° have more or less horizontally arranged apertures facing upward (Tajika et al. 2015; Naglik et al. in press).

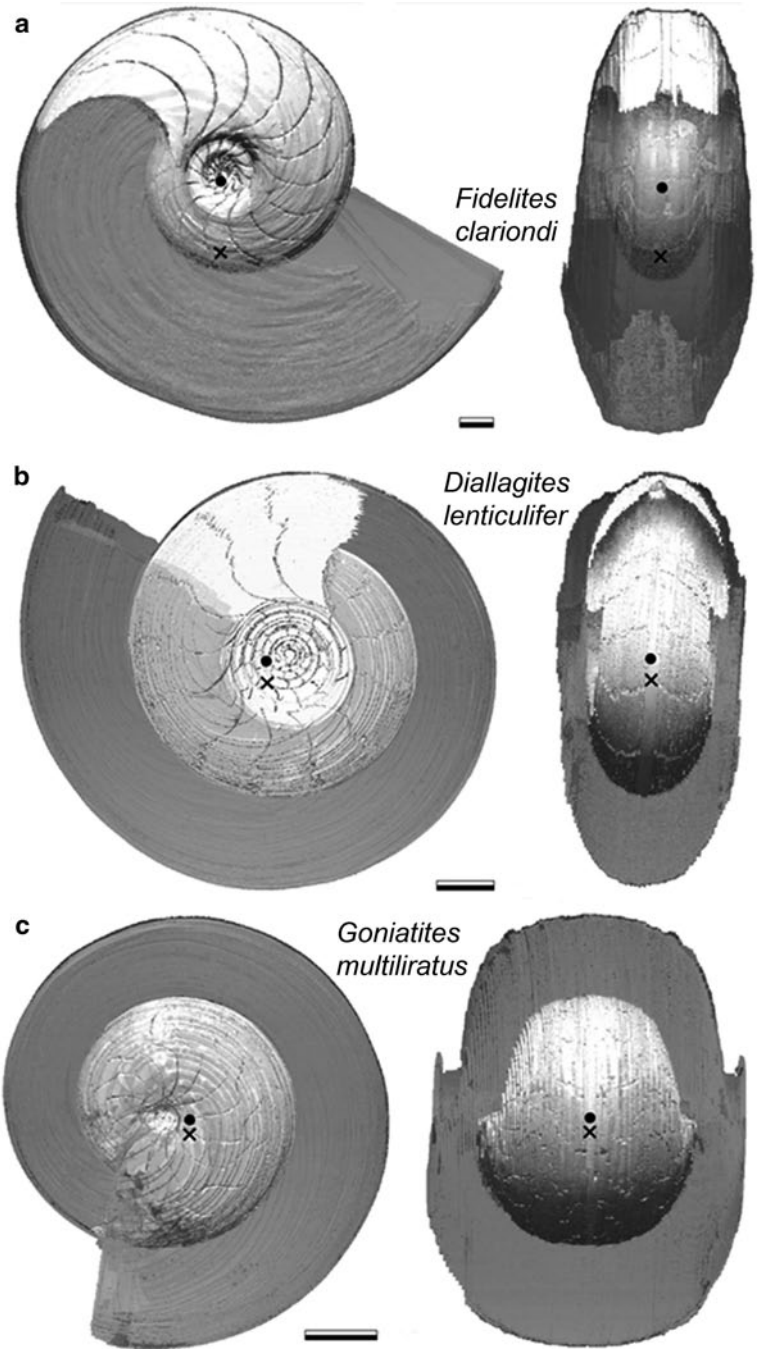

Fig. 17.5 Three Paleozoic ammonoids that have been subjected to grinding tomography in order to produce virtual 3D-reconstructions. Based on the image stacks, centers of mass (x) and buoyancy (o) were established based on these empirical models. (From Naglik et al. 2015). Scale bar: 0.5 cm

17.4 Muscles, Drag and Power

Because we cannot directly observe live ammonoids swimming, testing hypotheses on ammonoid swimming speed and swimming behavior presents obvious challenges to researchers interested in such matters. A wide variety of approaches to these issues are possible, but so far interest has centered primarily on muscles used to generate propulsion, drag, and power.

17.4.1 Muscles

Muscle attachment structures are reviewed by Doguzhaeva and Mapes (2015). According to them, jet-powered swimming could have been possible for forms with a body chamber length of one whorl or less and muscle attachments that would permit some muscles to extend straight across the body chamber and attach to the head and to the funnel.

A basic question here is the following: which of the extant cephalopods, if any, have a propulsive muscular system and mode of locomotion similar to that of ammonoids? The following kinds of muscular systems characterize modern cephalopods:

1. *Nautilus*-like: Because Recent nautilids are the only extant ectocochleate cephalopods, they have commonly been used as paradigms to understand the paleobiology of ammonoids. In modern nautilids, the large cephalic retractor muscles, which are attached to the inner shell wall of the body chamber, pull the head complex back into the body chamber, thus compressing the mantle cavity and expelling a propulsive jet of water out of the hyponome (Packard et al. 1980; Chamberlain 1981, 1987). The occurrence of apparent retractor muscle attachment scars in some ammonoids, as pointed out in Doguzhaeva and Mapes (2015), suggests that such ammonoids may have powered themselves by a "piston-pump" system not unlike what is seen in *Nautilus*.
2. Squid-like: Taking cephalopod phylogeny into account, ammonoids are more closely related to coleoids than to nautilids (Jacobs and Landman 1993; Kröger et al. 2011), and perhaps one may thus expect some similarities in coleoid and ammonoid propulsion systems. Modern squids use their muscular mantle (Bone et al. 1981) to pressurize mantle cavity water, which is then ejected through the funnel. However, the mantle in squids is not surrounded by shell as in *Nautilus*, or ammonoids, and does not function in shell secretion. It is generally considered that ammonoids also used their mantle to secrete the shell, as do ectocochleate cephalopods in general. Whether this necessarily implies that the ammonoid mantle was attached to the inner shell surface, and was secretory rather than muscular and incapable of compressing the mantle cavity is open to debate. In this regard, Jacobs and Landman (1993) as well as Jacobs and Chamberlain (1996) have suggested that the absence of large lateral muscle scars in some ammonoids

may mean that such animals used a squid-like system of propulsion involving the mantle. It has even been suggested that some ammonoids may actually have internalized shells (Doguzhaeva and Mutvei 1991, 1993), but in such cases, the mantle cavity was still located inside the body chamber of the shell. The *Nautilus* hyponome is also muscular and can direct and further compress the propulsive flow, but unlike the tubular funnel in coleoids, the *Nautilus* hyponome is a flap of tissue with folded, overlapping edges. Westermann (2013) proposed that some ammonoids may have had a powerful, coleoid-like tubular hyponome that was the main source of propulsive power. Nevertheless, the fins (probably not present in ammonoids) sometimes also play a role in squid locomotion (Packard 1972; Well 1995; Boyle and Rodhouse 2005)

3. *Argonauta*-like: Females of the octobrachian *Argonauta* produce an egg-case that is used both to shelter the eggs and to pick up air at the water surface in order to regulate buoyancy (Finn and Norman 2010). The shell differs from ammonoid shells in the absence of chambers and the fact that the *Argonauta* shell is secreted by two modified arms; other characters also differ (compare Hewitt and Westermann 2003). The mantle is not firmly attached to the shell and propulsion is carried out by means of the mantle as in other octobrachians (Young 1960; Finn and Norman 2010; Rosa and Seibel (2010).It is highly unlikely that ammonoids propelled themselves in a way analogous to that of a female *Argonauta*.
4. *Vampyroteuthis/Octopus*-like: *Vampyroteuthis* and several octobrachians can swim by contracting their arms with the velar skins, thus expelling water (Boyle and Rodhouse 2005). Since hardly anything is known about ammonoid arms (Klug and Lehmann 2015), it is currently impossible to conclude if such a mode of locomotion occurred in ammonoids.

In our view, it is likely, but not proven, that many ammonoids used longitudinal muscles to power jet propulsion. Evidence for the use of arms, velar webs, fins and mantle muscles in ammonoid locomotion is still poor or lacking. The possible efficiency, energy requirements and energy consumption associated with ammonoid propulsion are discussed in Chap. 17.4.3 below.

17.4.2 Drag

Drag is a physical term, which describes the forces that counteract the motion of an object moving through a fluid, namely seawater in the case of ammonoids. Drag is the product of the inertial and viscous forces acting on such an object, and thus depends on size, shape, and speed of the object, and on the density and viscosity of the fluid. Drag is one of the physical aspects of ammonoids that can be measured directly, even on fossil specimens (Schmidt 1930; Kummel and Lloyd 1955; Chamberlain 1976, 1980, 1981; Chamberlain and Westermann 1976; Jacobs 1992b; Jacobs et al. 1994; Jacobs and Chamberlain 1996). Drag force is usually measured directly, as was done in the studies noted immediately above. In situations where separated flow occurs, as would normally be the case for medium-sized and large

ammonoids moving relatively fast, drag can also be calculated from the following equation.

$$F_D = \tfrac{1}{2} \rho \, v^2 \, C_d A$$

F_D—drag force; ρ—density of the medium (seawater); v—velocity of the object (ammonoid); C_d—drag coefficient of the object (a dimensionless number which can be thought as representing the shape of the moving object); A—an area representative of the size of the moving object.

For objects, such as ammonoids, which have complex shapes, and thus complex flow interactions, shell volume raised to the two-thirds power ($V^{2/3}$) is generally the areal parameter of choice (Chamberlain 1976; Vogel 1981). It is important to understand that C_d is not a constant; it is a coefficient that varies widely for a given object depending on flow conditions. Flow state around an object, like an ammonoid, is described in terms of the Reynolds number.

$$Re = dm \, v / \upsilon \quad \text{with} \quad \upsilon = \gamma / \rho$$

Re—Reynolds number; dm—specimen shell diameter in the direction of motion; v—velocity of the object; υ—kinematic viscosity of seawater (viscosity [γ] divided by seawater density [ρ]). When Re is low (Re < 1000 approximately), flow is attached to the object (this is often referred to as Stokes Flow); drag is due entirely to surface friction; C_d is very high, often more than 100, and varies directly with velocity and Re. Spherical objects generate the least drag because they have the smallest surface area, and hence least frictional drag per unit volume. For ammonoids, these conditions would hold for small ammonoids swimming slowly. When Re exceeds approximately 10,000, flow is separated to some degree from the object (this is often referred to as separated or non-Stokes flow); drag is due to a combination of friction and an adverse pressure gradient created by the separation; and C_d is low and often constant, or nearly so, as Re and velocity change, fusiform objects generate the least drag because they have the smallest possible pressure drag component (fusiform shapes minimize the extent and magnitude of separation and the posterior low pressures that derive from separation). For many objects operating in separated flow, a large reduction in C_d occurs when the character of the fluid boundary layer lying on the surface of the object converts from laminar to turbulent conditions. For ammonoids, separated flow would hold for large ammonoids swimming quickly. At intermediate values of Re (1000 > Re < 10,000 approximately), flow is unstable and can vary from a separated to attached state depending on such factors as object shape and surface features. This would apply to ammonoids of intermediate size moving at intermediate speeds.

Several authors examined drag using ammonoid models (Schmidt 1930; Kummel and Lloyd 1955; Chamberlain 1976; Jacobs 1992b; Jacobs and Chamberlain 1996). Modeling focused on the shell only (Kummel and Lloyd 1955; Chamberlain 1976); the shell and attached prostheses imitating extruding soft parts (Chamberlain 1980); or shell and artificial surface sculpture (Chamberlain 1981). For models

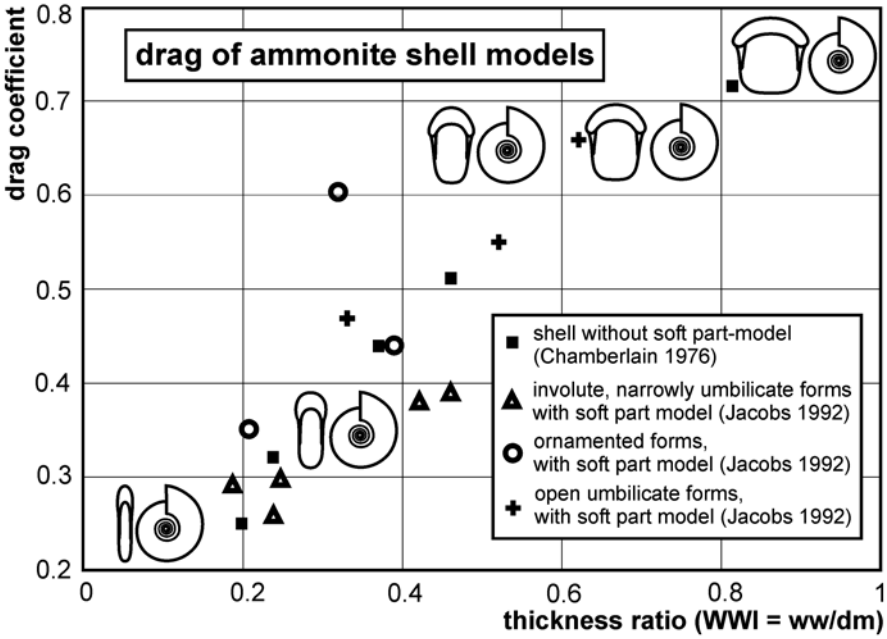

Fig. 17.6 Relationship between the thickness ratio and the drag coefficient, depending to a lesser degree on other factors such as umbilical width and ornament strength. These data (Chamberlain 1976; Jacobs 1992b) were obtained from models in a water tank (modified after Jacobs and Chamberlain 1996)

with representative values of Raup's W and D values (Raup 1966, 1967; Raup and Chamberlain 1967), Chamberlain (1976) determined drag coefficients in separated flow (i.e. for higher velocities and larger shells) where pressure drag is the key hydrodynamic factor. These experiments on models revealed that narrower shells had lower drag values. It appears to be mainly shell thickness and umbilical width, which play important role in generating drag in such flow conditions (Fig. 17.6).

In a later study, Jacobs (1992b) focused on drag for ammonoids of small size and low velocity (Re below about 25000), where frictional drag is the key hydrodynamic factor (see also Jacobs and Chamberlain 1996). Some results of Jacobs (1992b) are reproduced in Fig. 17.7. Note that in each graph in Fig. 17.7, the curves for wide and narrow forms cross at a point between Reynolds numbers of 5000 and 10,000. At Re less than the crossing value, the wider shells have lower drag coefficients (less frictional drag in Stokes flow) than the narrow shells, but at Re greater than the crossing value, the narrow shells have lower drag coefficients (less pressure drag in separated flow). This implies that different shell morphologies are more efficient at different sizes and swimming speeds (Table 17.1). Narrow forms produce less drag than wide forms at higher Reynolds numbers (faster speeds, larger size), while wide shells generate less drag at low Reynolds numbers (slower speeds, smaller size) than do narrow shells. This situation implies that the com-

Table 17.1 Possible swimming behavior of ammonoids in dependence of their shell shape. (Modified after Jacobs and Chamberlain 1996). For *Baculites*, we used the interpretation of Westermann (2013). Additional information comes from Klinger (1981) and Seki et al. (2000)

Shell shape	Slow, continuous swimming	Fast, continuous swimming	Acceleration	Vertical
Compressed involute				
Oxyconic (e.g., *Sphenodiscus*)	Poor	Good	Excellent	Moderate
Platyconic with rounded venter (e.g., *Oppelia*)	Moderate	Excellent	Good	Moderate
Platyconic with tabulate venter (e.g., *Anahoplites*)	Good?	Good	Moderate	Moderate
Moderately compressed				
Platyconic, moderately evolute (e.g., *Mesobeloceras*)	Moderate	Good	Moderate	Moderate
Involute juvenile (e.g., *Scaphites*)		Moderate	Moderate	Moderate
Evolute, rounded whorls (e.g., *Lytoceras*)	Moderate	Moderate	Poor	Moderate
Compressed evolute	Good	Moderate	Moderate	Good
Depressed				
Sphaeroconic involute (e.g., *Goniatites*)	Moderate	Poor	Poor	Moderate
Cadiconic, evolute (e.g., *Cabrieroceras*, *Gabbioceras*)	Moderate	Poor	Poor	Moderate
Heteromorphic				
Orthoconic (e.g., *Baculites*)	Moderate	Moderate	Excellent?	Moderate
Torticonic (e.g., *Turrilites*)	Poor	Poor	Poor	Good
Loosely coiled in three dimensions (e.g., *Nipponites, Didymoceras*)	Poor	Poor	Poor	Good

mon ammonoid ontogenetic change in shell morphology from depressed juvenile whorls to more compressed whorl shape near maturity could be linked with this flow state dependent change in drag coefficient (Jacobs and Chamberlain 1996). The latter authors also suggested that morphologic change related to hydrodynamic factors operating in the evolution of ammonoid clades should be linked with different host facies. This link was examined by various authors (e.g., Ziegler 1967; Batt 1989; Bayer and McGhee 1984; Marchand 1992; Courville and Thierry 1993;

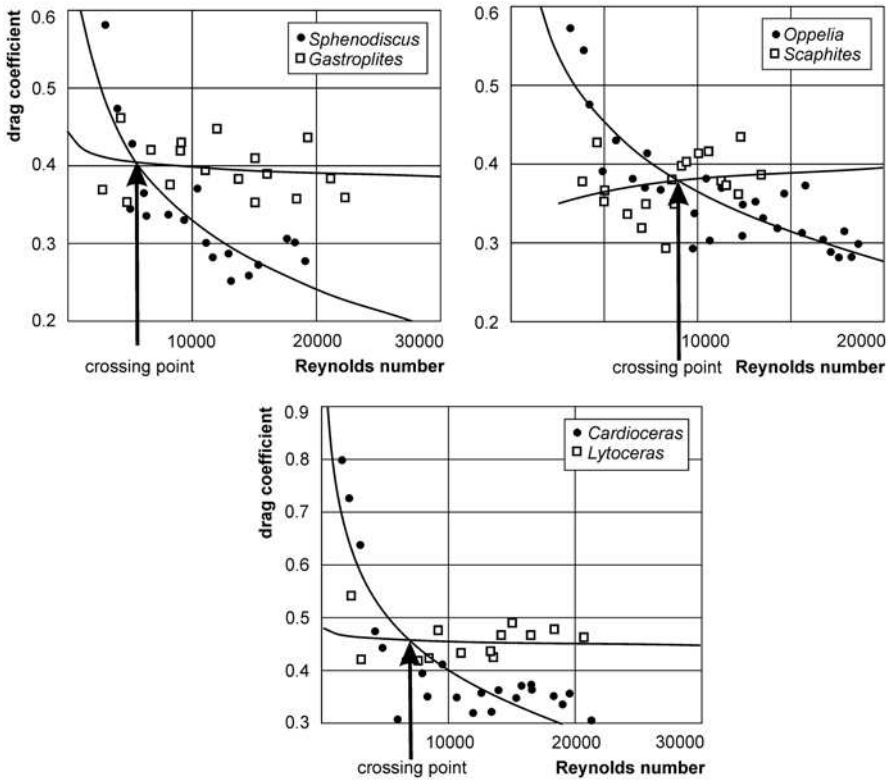

Fig. 17.7 Relationships between drag coefficients and Reynolds number (Re) of three different pairs of Jurassic and Cretaceous ammonoids. In each pair, one form has a narrow shell (*dots*), and one has a wide shell (*open squares*). Note that in each graph the curves for the two forms cross at a point between Reynolds numbers of 5000 and 10000. At Re less than the crossing value, the wider shells have lower drag coefficients (less frictional drag in Stokes flow) than the narrow shells, but at Re greater than the crossing value, the narrow shells have lower drag coefficients (less pressure drag in separated flow)

Jacobs et al. 1994; Klug 2002; Kawabe 2003). Such studies are hampered by the possibility that ammonoid shells were transported post mortem and the imperfect knowledge of habitat depth, because the sedimentary context in which ammonoids are preserved mainly informs about the energy in the water column and the volume of sediment that is delivered in combination with accommodation space. It is possible that ammonoids could have lived in more quiet waters near the sea-floor or in more agitated waters near the surface uncharacteristic of the sedimentary context of the rock itself. Additional factors, such as time-averaging might also complicate straight forward interpretations (compare De Baets et al. 2015a).

In any case, the measurable disparity of ammonoids throughout ontogeny and evolution as well as the recurrent ontogenetic change in shell shape indicate that minimizing drag played an important role in ammonoid evolution. It also indicates

that different forms were possibly specialized for different modes of life with correspondingly different swimming abilities.

17.4.3 Power

The use and availability of power for swimming in ammonoids cannot be measured directly and thus has to be addressed based on actualistic comparisons with living organisms (e.g., Trueman and Packard 1968).

The physical term, power, simply describes the ratio between the work, W, expended in a time interval, t:

$$P = \Delta W / \Delta t$$

Assuming constant velocity during the time interval in question, this can be modified to the following equation using drag force F_D and velocity v:

$$P = F_D \, v$$

Power consumption during swimming thus depends directly on drag coefficient and can be estimated from the relationship between drag coefficient and Reynolds number, and thus with respect to size and velocity (Jacobs 1992b; Jacobs and Chamberlain 1996). In order to assess the differences in power consumption as a function of shell form, size and velocity, Jacobs (1992b) produced drag data for the thick genus *Gastroplites* (ww/dm = 0.42) and the thin genus *Sphenodiscus* (ww/dm = 0.19). His results are reproduced here in Fig. 17.8. According to Fig. 17.8, *Gastroplites* would require less power at sizes below 10 cm and velocities below 50 cm/s. At a shell size of 10–100 cm and speeds below 15 cm/s, the two shell shapes would require about the same power. At higher speeds and sizes exceeding 10 cm, *Sphenodiscus* would need less power and swim more economically. Whether these ammonoids could actually produce the power necessary to swim at these speeds cannot be inferred from such data, however.

Knowledge of swimming speed in fossil ammonoids requires knowledge of the power output generated by live ammonoids. The power produced by live ammonoids is unknown. However, one can gain useful insight into this matter by applying to this question data on power output of modern swimmers, particularly modern cephalopods. Of primary interest is the power output of modern analogues in sustained swimming (powered by aerobic muscle contraction), and in burst swimming (powered by anaerobic muscle contraction). Also of interest is metabolic scope, i.e., the difference between the power requirements during inactivity and periods of maximum activity. Unsurprisingly, power output and metabolic scope differ strongly between living cephalopods such as *Nautilus* with very low metabolic rates and the active squid *Illex* with a high metabolic scope (O'Dor 1982, 1988a, b; Chamberlain 1987; O'Dor and Wells 1990; O'Dor et al. 1990, 1993; O'Dor and Webber 1991). Even among squids, metabolic rates can vary strongly depending on

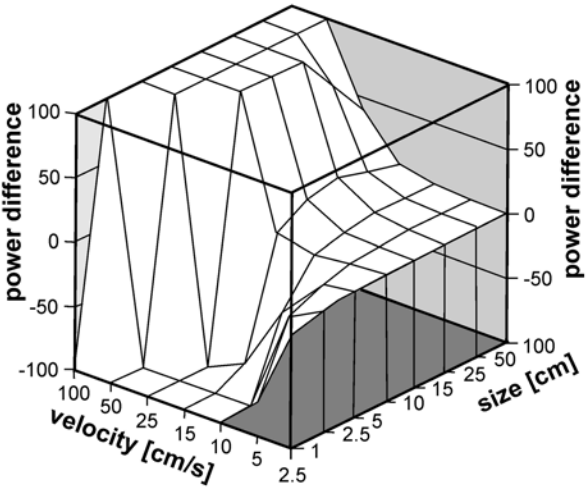

Fig. 17.8 Differences in power consumption (in ergs/s/cm^3) in a broad, depressed form (*Gastroplites*) and in a narrow, laterally compressed form (*Sphenodiscus*). Power difference was calculated by subtracting the power required per unit volume in *Sphenodiscus* from that of *Gastroplites*. Depending on this ratio, one obtains positive or negative values: when the values of power difference are negative, *Gastroplites* requires less power. The greatest power difference is seen at low sizes and high velocities. Jacobs and Chamberlain (1996) considered these differences as so profound that they appear to be biologically significant. Power differences > 100 ergs/s/cm^3 are not shown (modified after Jacobs and Chamberlain 1996)

their habitats (Seibel et al. 1997). For instance, the deep-sea squid *Vampyroteuthis infernalis* has a metabolic rate a hundred times lower than the shallow water *Gonatus onyx* (Seibel et al. 1997).

Estimates of power production in ammonoids depend on whether Recent nautilids are considered the better model organisms with their similarly constructed external shell or whether coleoids should rather be used as paradigms because they are more closely related to ammonoids. Several authors (e.g., Trueman 1941; Swan and Saunders 1987; Jacobs and Landman 1993; Kröger et al. 2011) have argued in favor of coleoids rather than nautilids on the basis of shell form and phylogeny. In order to estimate sustainable swimming speeds in ammonoids, Jacobs (1992b) argued that a metabolic rate of 200 ml of oxygen per kilogram per hour, which is close to that of *Sepia* (O'Dor and Webber 1991), probably represents a reasonable figure for most ammonoids. He also advocated that for ammonoids, sepiids represent the most meaningful model organisms among coleoids because like ammonoids, they have a large chambered phragmocone, which greatly limits the relative proportion of propulsive muscle (and soft tissue generally) to total volume of the animal (see also Chamberlain 1981, 1990, 1992, 1993). By comparison, squids like *Illex*, pack their bodies much more fully with propulsive muscle. O'Dor and Webber (1991) found that the metabolic scope of the highly active *Illex* was four times larger than in *Sepia* and additionally, the efficiency of their muscles exceeds that of sepiids. In

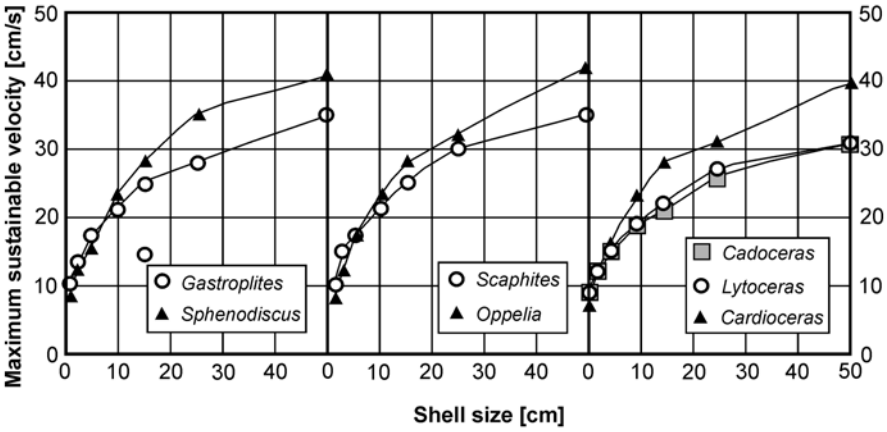

Fig. 17.9 Maximum sustainable swimming velocities in seven ammonoid genera. These are arranged in groups of two or three, always comprising a genus with a more compressed and one with a more depressed shell form. The velocity values are based on the assumption that the maximum power availability was 400 ergs/s/cm^3. Overall, the curves resemble each other and in the curve pairs, they cross each other at a size of 5 to 10 cm (modified after Jacobs (1992b) as well as Jacobs and Chamberlain (1996))

consequence, power output is ten times higher in *Illex*, thus making *Sepia* the better actualistic model organism for ammonoids (Jacobs and Chamberlain 1996).

O'Dor and Webber (1991) observed swimming speeds of maximally 65 cm/s (2.3 km/h), which required a power output of 1000 μJ/s/cm^3. Jacobs (1992b) as well as Jacobs and Chamberlain (1996) concluded that in ammonoids, this figure would probably not have exceeded 600 μJ/s/cm^3 because only about 40 % of the organism's volume is occupied by soft parts. The maximum swimming speeds of some ammonoid species, which are based on these assumptions, are depicted in Fig. 17.9. Maximum swimming speeds of large ammonoids like *Sphenodiscus* with a shell diameter of 25 cm would not have exceeded 100 cm/s (3.6 km/h). *Gastroplites* of the same size would have a speed of about 70 cm/s (2.5 km/h). The latter velocity corresponds to the maximum in *Sepia* (Jacobs and Chamberlain 1996). As a lower limit of energy availability, *Nautilus* can be used as model. Nautilus can activate up to 100 μJ/s/cm^3, i.e. a tenth of that of *Sepia*. Using this figure, a 25 cm *Gastroplites* could reach 40 cm/s (0.54 km/h) and *Sphenodiscus* would have been able to swim 55 cm/s (1.98 km/h). These results are similar to swimming velocity estimates based primarily on drag considerations made by Chamberlain (1981, Fig. 17.8).

In summary, Jacobs (1992b) as well as Jacobs and Chamberlain (1996) found that swimming speed of ammonoids likely depended on various factors including shell shape (e.g. Table 17.1), body chamber angle, size, energy availability and power consumption. For large size, ammonoids with compressed shell form (low ww/dm ratio) could swim faster than those with depressed shells (high ww/dm ratio); while at small size this relationship is reversed.

17.4.4 Acceleration

Accelerating an object in a fluid involves accelerating fluid entrained in the object's wake and also fluid in direct contact with the surface of the object, i.e. in the boundary layer. In the case of swimming organisms, this also applies and in order to estimate swimming speeds and energy requirements, this added mass has to be taken into account (Chamberlain 1987; Jacobs 1992b; Jacobs and Chamberlain 1996). The force required to accelerate this added mass can be quantified by the following equation, which was introduced by Daniel (1984):

$$G = -ar\,V\left(du/dt\right)$$

G—acceleration reaction force; a—added mass coefficient (a function of thickness ratio ww/dm); r—density of the fluid; V—volume of the object/ammonoid; du/dt—acceleration.

The acceleration reaction force occurs both in acceleration and deceleration (Daniel 1984; Chamberlain 1987; Jacobs 1992b; Jacobs and Chamberlain 1996). For ammonoids, the symmetry of the shell in swimming direction, shell shape, differences in acceleration and deceleration processes as well as the formation of vortices in the wake play a role.

In cephalopods, acceleration is produced by a series of water expulsions from the hyponome with interim phases of water intake into the mantle cavity. The animal accelerates when the propulsive muscles contract forcing water from the mantle cavity and decelerates during the recovery phase of the propulsive cycle when water is taken into the mantle cavity in preparation for the next mantle cavity contraction. When an organism starts swimming, energy is mainly invested in acceleration while at higher speeds when velocity is more constant, the energetic cost of drag rises. Acceleration force also depends on the width of the ammonoid shell (ww/dm ratio; Fig. 17.10) and it roughly doubles from ww/dm = 0.2 to a value of 0.4 (Jacobs and Chamberlain 1996). According to Daniel (1984, 1985), the ratio of energetic costs of drag to that of acceleration varies from 48 % in a small squid accelerating from 0 to 2000 cm/s^2 to 62 % in a medusa accelerating to 700 cm/s^2 to 92 % in a salp accelerating to 23 cm/s^2. These values show that the faster an organism accelerates to a higher velocity, the lower the relative energy investment into added mass and the higher the investment into overcoming drag.

This relationship points to a potentially multiple functions of shell shape in ammonoids. While some shell morphologies reduced drag, other shell morphologies, such as oxycones with a small umbilicus, would have reduced the energetic cost invested in added mass (Jacobs 1992b; Jacobs and Chamberlain 1996). In that respect, ammonoids with narrow oxyconic shells would resemble ambush predators among fish (e.g. pike, barracuda) whose body geometry is too elongate to be purely adapted to reduce drag. Instead, their long and narrow shape strongly reduces acceleration reaction force and enables them to accelerate strongly from a standing start. While there is no corroboratory evidence for an ambush predator strategy

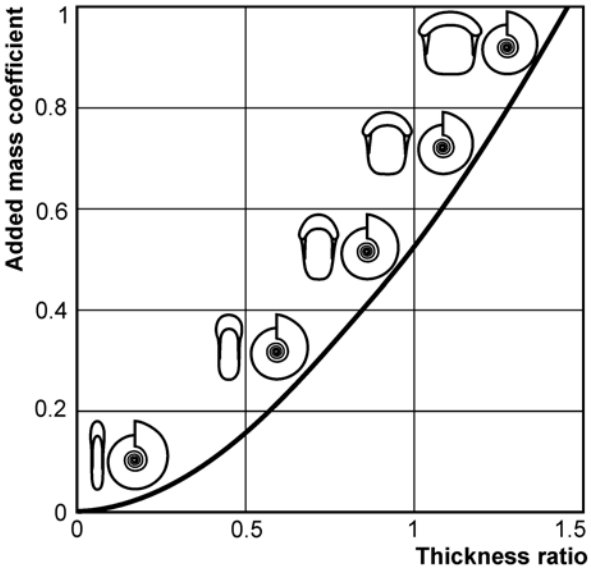

Fig. 17.10 Depending on shell shape and ornament, differing amounts of added mass of water accelerated with the ammonoid in the boundary layer and the wake can be expected. The acceleration reaction is a linear function velocity change (acceleration) and a function of the added mass coefficient, which -in turn- depends on shell shape and orientation relative to the direction of acceleration. According to these relationships, ammonoids with laterally compressed shells had substantially less added mass than ammonoids with depressed shells (modified after Jacobs (1992b) as well as Jacobs and Chamberlain (1996))

in oxyconic ammonoids, the fact that oxyconic shell form evolved many times iteratively and sometimes even in parallel (e.g., Bayer and McGhee 1984; Klug and Korn 2002; Monnet et al. 2011) shows that this shell shape may indeed have had a positive adaptive benefit for ammonoids.

17.4.5 Cost of Transportation

The cost of transportation (COT) is a metric that describes the energetic cost of locomotion. COT has been defined in a variety of ways. For example, in his comparison of the energy cost of different styles of animal locomotion Schmidt-Nielsen (1972) defined COT as (metabolic rate/(body weight and speed). O'Dor (1988a) and O'Dor and Webber (1991) in their study of squid locomotion, and Chamberlain (1990) in his study of *Nautilus* locomotion, determined COT by calculating metabolic output from oxygen consumption data for swimming animals. In all such approaches the aim has been to express COT in terms of the propulsive power produced by a swimming animal relative to some measure of its size, speed, and distance travelled. COT is thus simply stated in terms of propulsive power per unit of animal size per unit of speed or distance traveled where animal size is represented by weight or volume.

The power produced by a swimming ammonoid can be expressed as follows:

$$P = W/t = (F\ d)/t = F\ v$$

where P is the metabolic output (power) used to produce locomotion; W is the work needed for locomotion; t is the time interval over which the locomotion occurs; F is the force or thrust developed by the swimming ammonoid and is assumed to be constant over the interval t; d is the distance traveled; and v is the animal's velocity, also assumed to be constant.

Jacobs (1992b) and Jacobs and Chamberlain (1996) used the power-required data and the efficiency assumptions of Jacobs (1992b) to evaluate COT for a few representative ammonoids. Following Jacobs (1962b), they calculated COT as propulsive power per unit of total shell volume per unit of distance traveled. Their results are diagrammed in Fig. 17.11. The upper panel in this figure indicates that, assuming *Sepia* metabolic output, *Gastroplites* COT depends on size. Larger animals have lower COTs for a given velocity than smaller ones. This is largely the result of larger animals operating in separated flow where drag coefficients are smaller while small animals operate in Stokes flow where drag coefficient is much higher for objects of the same shape. The upper panel also indicates that if we assume *Gastroplites* had a lower metabolic output equivalent to that of *Nautilus*, its COT would also be lower. Perhaps the most interesting observation to be made from Fig. 17.11 is that for each curve there is a specific velocity for which COT is minimal. If energy conservation in swimming ammonoids mirrors that of flying animals, where flight speed usually reflects minimal COT, and there is no reason why it should not, this may mean that this minimal COT speed represents the usual swimming speed for the ammonoid to which the curve applies. The steepness of the curve on either side of the minimum COT speed implies that there would be considerable gain in cost to the animal in moving away from this optimum speed. The lower panel in Fig. 17.11 shows that the modern swimmers plotted here, both coleoids and fish, have COT-velocity curves much less steeply inclined as velocity increases above the minimum COT speed. This means that these modern animals are not nearly so constrained in terms of COT in varying their swimming speed than is the case for the ammonoids plotted here as well. Swimming over a range of velocities does not greatly influence their COT. It would appear that these modern swimmers have a much more flexible swimming repertoire than did fossil ammonoids.

Jacobs (1992b) as well as Jacobs and Chamberlain (1996) suggested that due to their neutral buoyancy, ammonoids, like *Nautilus*, may have had a low use of energy at rest and that the cost of transportation in ammonoids was accordingly low at low velocities. Alternatively, if ammonoids were closer to sepiids in their metabolic rates, the cost of transportation would have been lower at higher swimming speeds depending on their size (Fig. 17.11). Jacobs and Chamberlain (1996, p. 210) summarized this idea as follows: "*ammonoids may not have been pursuit predators, comparable to tuna or some squids, that spend long periods of time chasing down prey at high speed. This would deny the utility of the neutrally buoyant shell in limiting energetic expenditure. However, life styles that require only intermittent bursts*

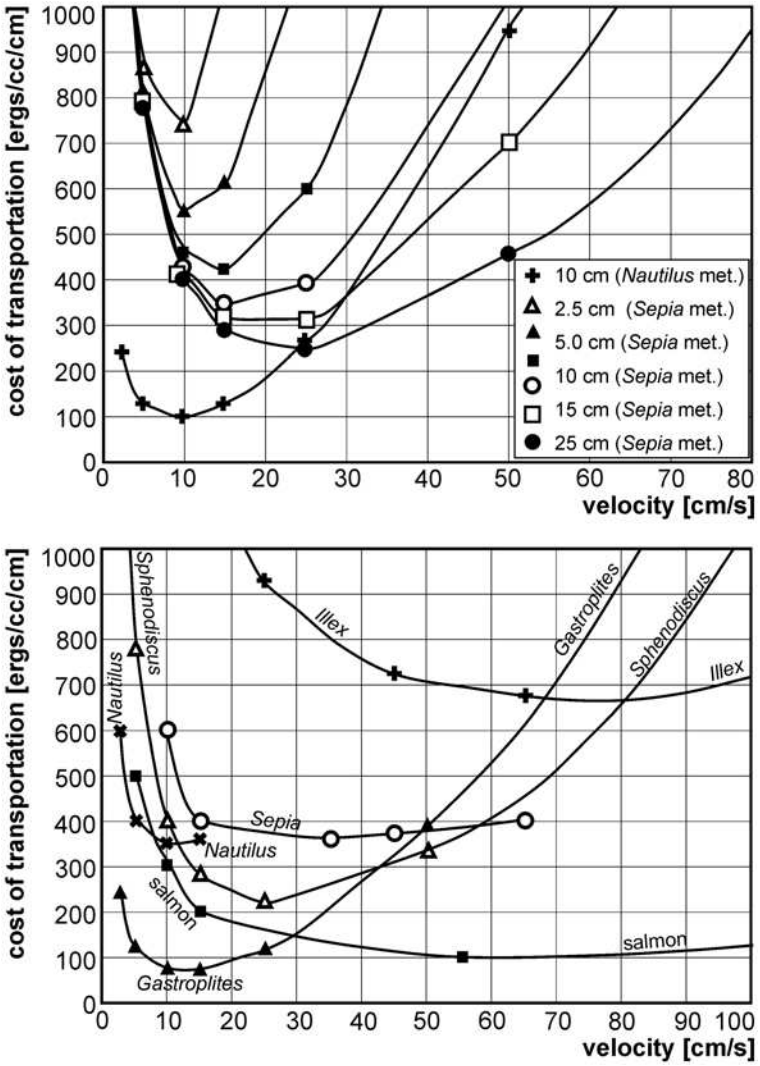

Fig. 17.11 Cost of transportation (*COT*) in relation to velocity depends on shell size and metabolic rate (upper diagram) and differs between modern animal groups (lower diagram). Modified after Jacobs (1992b) as well as Jacobs and Chamberlain (1996). The efficiency of energy conversion into propulsion force is estimated to be 10 %. The upper diagram shows the COT for various sizes of *Gastroplites*, assuming metabolic rates (O'Dor and Webber 1991) of *Sepia* (3900 ergs/s/cm^3) and in one case of *Nautilus* (1/7th of *Sepia*). With increasing size, less energy is required for locomotion. The lower diagram shows the COT of *Sphenodiscus* and *Gastroplites* in comparison to various recent cephalopods and a fish (O'Dor and Webber 1991). Resting metabolic rates were estimated for *Sphenodiscus* to resemble that of *Sepia* and for *Gastroplites* to resemble that of *Nautilus*. At higher velocities, the costs rise much faster in the shelled swimmers than in fishes and squids. However, the ammonoid curves are based on a series of estimates for the metabolic rates, added mass and other modes of locomotion (fins in *Sepia*)

of energy, such as ambush predation, seem possible, and oxyconic shell shape […] *may have been conducive to such a mode of life*." It should be remembered that high speed is not required for successful predation. A predator must only move faster than its prey. If its prey is slow, a predator can be slow also. Oxycones would not need the fast burst speed of *Illex* or *Sphyraena* (barracuda) to prey on slower moving ammonoids.

Jacobs (1992b) and Jacobs and Chamberlain (1996) also pointed out that energy used for transport is energy that cannot be used in other ways; there is a trade-off between these costs and the energetic cost of other life functions. Nautilids have a low metabolism and can fast over lengthy time spans. In such a case, slow swimming speeds (O'Dor et al. 1990) are advantageous in promoting prolonged food searches (Wells 1987; Chamberlain 1990; Jacobs and Chamberlain 1996), as is the case for *Nautilus* (Ward and Wicksten 1980). Wells and O'Dor (1991) thought that other ectocochleates such as ammonoids may have pursued a similar low energy mode of life. They supported this hypothesis by pointing out that increasing numbers of fish occupied high energy nektonic habitats (for these macroecological changes, see Signor and Brett 1984; Bambach 1999; Kröger 2005; Klug et al. 2010) and would have competitively excluded most ammonoids from these habitats. The problem with this hypothesis is twofold: (1) As Jacobs and Chamberlain (1996) pointed out, ammonoids are more closely related to coleoids (some of which use considerable energy in relation to body size and also swim at high velocities) than they are to low energy nautilids (Jacobs and Landman 1993; Kröger et al. 2011). (2) The radiation of gnathostome fish in the Silurian and Devonian, a major event in the evolution and history of diversification of fishes, was also a time in which ammonoids originated and rapidly diversified (Klug et al. 2010). The diversification of teleostean fish in the Mesozoic also appears to be largely independent of ammonoid diversity changes (Jacobs and Chamberlain 1996), although the Cretaceous diversification of deep-bodied acanthopterygians may have been a factor influencing ammonoid diversity late in their history (Chamberlain 1993). Some heteromorphs might have been slower swimmers than nautilids in horizontal direction, although this requires further research (e.g., Ward 1979; Westermann 1996).

17.4.6 The Role of Ornament

As in sharks (Reif 1982; Oefner and Lauder 2012) and golf balls, a fine regular surface ornament can reduce drag by forcing conversion of the boundary layer around an ammonoid shell from laminar to turbulent flow at lower Reynolds numbers than would normally be the case. Boundary layer conversion reduces the scale of the turbulent wake and the pressure drag that results from it. Chamberlain and Westermann (1976) and Chamberlain (1981) examined this phenomenon and concluded that it could have a positive effect for some ammonoids by bringing lower drag and more efficient swimming into the velocity range of some ammonoids. Nevertheless, the lowering of the coefficient of drag would have been significant at Reynolds numbers exceeding 40,000, a figure that could potentially only be achieved in large ammonoids moving at relatively high velocities (Chamberlain 1981).

Jacobs and Chamberlain (1996) speculated that in cadicones, the coarse ribs or nodes as in *Cabrieroceras*, *Gastrioceras* or *Teloceras* might have caused the formation of vortices covering the entire umbilicus. Similarly, they suggested that, in forms with tabulate venter (or with ventral band as in Devonian forms such as *Gyroceratites*, *Armatites* or *Kosmoclymenia*), the water might have been divided into two fields, thus maintaining flow attachment and reducing turbulence in their wake, at least at certain velocities and sizes. They also reasoned that ribs tend to be the largest near the aperture and to be oriented in swimming direction, thus stabilizing the shell orientation during backward swimming in forms, which are more or less involute and carry moderately strong ribs such as *Cardioceras*. Westermann (1966) even speculated that this might be a driving force behind Buckman's law of covariation, although this law can be conveniently explained by morphogenetic processes (Monnet et al. 2015) without an adaptive interpretation (compare Hewitt 1996 for an alternative functional explanation). In contrast, strong ornament significantly increased drag (Chamberlain 1976; Jacobs 1992b; Hewitt 1996; Jacobs and Chamberlain 1996), thus supporting indirectly its possibly defensive function shell sculpture (e.g., Ward 1981).

17.4.7 Hydrodynamics Through Ammonoid Development

As discussed in Hoffmann et al. (2015), the flow regime in which ammonoid swimming took place changed through ontogeny as ammonoids grew in body size and shell diameter. Ontogenetic size increase covered two orders of magnitude or more in most ammonoid taxa. While embryonic shells (Landman et al. 1983; De Baets et al. 2012) vary about one order in magnitude in size between the earliest forms (>5 mm) and several derived Mesozoic forms (ca. 0.5 mm), the adult shells vary from less than 1 cm to over 2 m. Because small individuals have less power in relation to drag, adult ammonoids could probably swim one to two orders of magnitude faster than hatchlings (Jacobs and Chamberlain 1996).

In hatchlings, much of the energy invested in locomotion will be absorbed by skin friction drag. Jacobs and Chamberlain (1996) guessed that a hatchling of 1 mm diameter might have attained a swimming speed of 1 cm/s, which corresponds to a Reynolds number near 10. Accordingly, shells with a high whorl width index would have been favorable. In that light, the common decrease in whorl width index, which occurs at that size, appears less surprising (Fig. 17.12). Jacobs and Chamberlain (1996) assumed that added mass and acceleration was more important for small than for large individuals. Consequently, early ontogenetic stages would have profited more from compressed shell shapes, which would have reduced the energetic cost of the acceleration reaction. Taking limited energy resources into account, it becomes clear that hatchlings and early juveniles were limited in most cases to a rather passive, probably planktonic mode of life. Residence of early ontogenetic stages in the water column is evidenced by ammonitellae and early ontogenetic stages of ammonoids in black shale deposits (e.g., Landman 1988; Mapes and Nützel 2008) and other lines of evidence (Landman et al. 1996; Ritterbush et al. 2014; De Baets et al. 2015c).

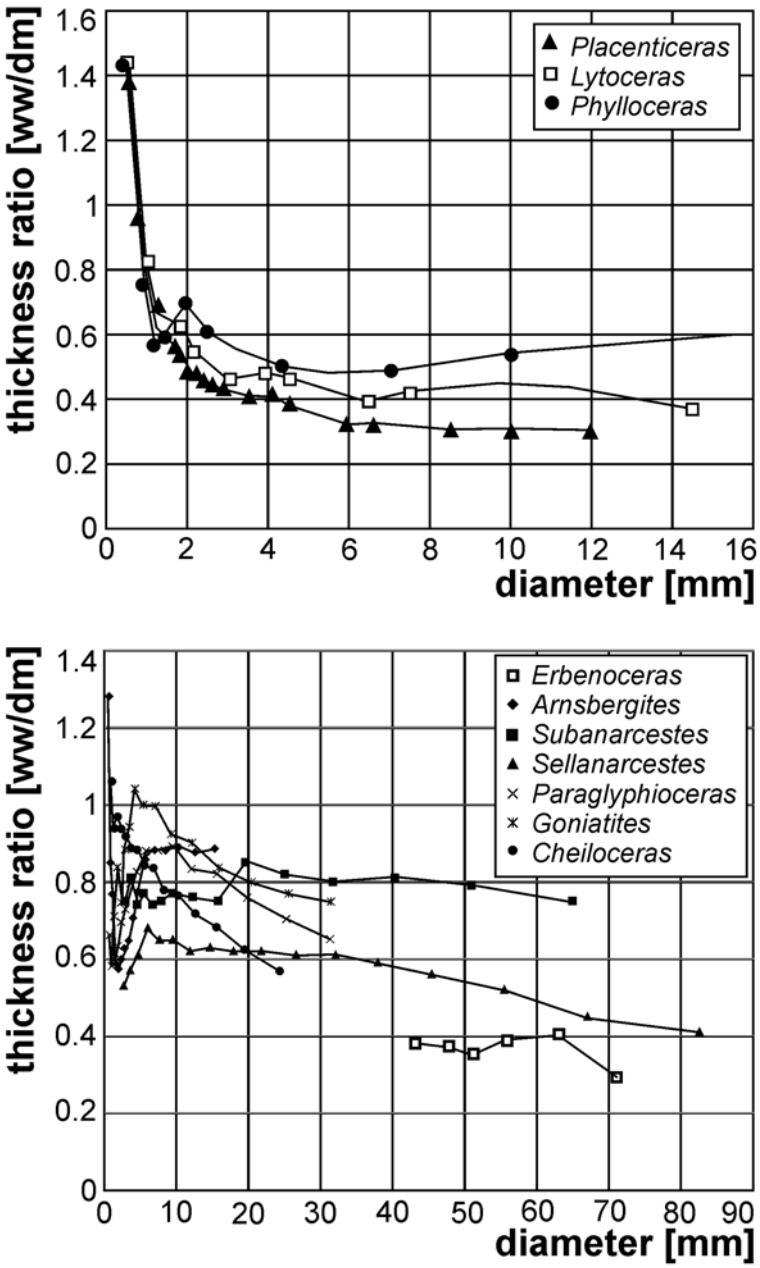

Fig. 17.12 Thickness ratio and shell size in Mesozoic (*top*) and Paleozoic ammonoids (*bottom*) through ontogeny. Modified after Jacobs (1992b) as well as Jacobs and Chamberlain (1996) with new data first reported here. Between hatching (dm < 5mm) and the end of the neanic stage (ca. 10 mm), ammonoids moved only slowly and had wide shells and thus swam at low Reynolds numbers. In all ammonoids, whorl width is reduced after the neanic stage, in Mesozoic forms to values between 0.3 and 0.6 and in Paleozoic forms to values between 0.3 and 0.8. These observations suggest that the ontogenetic late neanic change in shell shape may be an adaptation reflecting the change in hydrodynamic flow conditions

Such accumulations of early ontogenetic stages have often, although not exclusively, been found from the Devonian to the Cretaceous in strata, where benthic life was strongly limited (compare De Baets et al. 2015c). Jacobs (1992b) suggested that the serpenticonic shell shape commonly found in ammonoids (Raup 1967) permitted ammonoids to optimize shell shape for swimming as Reynolds number increased during growth. In contrast, most nautilids (except the aturiids) avoided the smallest size-range for their juveniles, which would have forced the juveniles into a passive planktonic mode of life and similarly, serpenticonic shell shapes are absent in post-Paleozoic Nautilida. Because of these poor locomotory capabilities of ammonoid hatchlings, Jacobs and Chamberlain (1996) considered the possibility of brood care in ammonoids, which finds some support in the occasionally extreme size-dimorphism among ammonoids (e.g., in scaphitids; compare De Baets et al. 2012; 2015c). Walton et al. (2010) speculated on brood care in the Late Devonian genus *Prolobites* based on the extremely low body chamber and terminal aperture, but in this case perhaps outside of the shell of the brooding adult.

Independent of the presence or absence of brood care in ammonoids, the profound morphologic changes that occur around hatching, at the end of the neanic stage, and at maturity (e.g., Westermann 1996; Klug 2001; Korn and Klug 2003) likely had effects on the physical framework for locomotion. It is also striking that commonly, morphologic changes occur at shell diameters between 1 and 2 cm, i.e., when active swimming became feasible for the young ammonoids.

17.5 Information from Epizoans

Some sessile organisms are known to attach themselves in an oriented way depending on the prevailing current direction. Ammonoid shells are well-known to have been inhabited by numerous different invertebrates *syn vivo* (Seilacher 1960; Davis et al. 1999). Some of these epizoans have accordingly been used to interpret the predominant swimming direction of ammonoids. For example, Seilacher (1960) showed bivalve overgrowth on *Buchiceras*, which supported an oblique upward orientation of the aperture of this Cretaceous ammonite.

Keupp et al. (1999) Seilacher and Keupp (2000) as well as Keupp (2012) described a Tithonian aspidocerid inhabited by numerous cirripeds. These epizoans likely attached themselves to the shell of the living ammonite because its aptychi are still in the body chamber and the cirripeds are well articulated. The feeding appendages point in the direction of the aperture, thus suggesting forward swimming, i.e. not backward, as it is usually done by modern cephalopods. This is consistent with the interpretations of Parent et al. (2014) regarding the effect of the aptychi in this genus on swimming speed and swimming direction. Forward swimming would have the advantage that the low hydrodynamic stability of many ammonoids would not have played a big role, because the ammonite shell would have followed the propellent.

Hauschke et al. (2011) described the oriented attachment of a cirripede (goose neck barnacle) on a baculitid. Their findings support forward swimming, but there is also some indication for an approximately horizontal shell orientation during

swimming of this orthoconic ammonite. Westermann (2013) contradicts this interpretation, arguing that these cirripedes might actually have colonized shells without a clear preference of orientation and because he thinks that the apical parts of the phragmocones were largely free of chamber water at such early ontogenetic stages. In addition with the rather long body chambers, it would have made young baculitids swim with their shells in a more or less vertical position.

17.6 Facies of the Host Rock and Habitats

It is one of the classical arguments in cephalopod paleobiology as to whether the host rock facies of a cephalopod fossil can be considered as an indicator of habitat in the live animal. The main reason for doubting the usefulness of studies on the rocks that contain ammonoids is the likelihood of post mortem transport (e.g., Kennedy and Cobban 1976; Tanabe 1979; Marchand 1984). Post mortem transport of nautilids over thousands of kilometers has been shown by various authors (Iredale 1944; Hamada 1964; Stenzel 1964; Toriyama et al. 1965; House 1973, 1987; Chirat 2000). In contrast, Chamberlain et al. (1981) argued that the strong pressure gradient between phragmocone chambers and ambient pressure in modern *Nautilus* leads to rapid post mortem waterlogging of the shell in animals dying within the normal depth range of the live animals (100–300 m). This would rapidly produce negative buoyancy and cause the empty shell to sink, thus precluding significant post-mortem drift (Maeda and Seilacher 1996). Animals dying at shallow depths would have a much greater chance of reaching the ocean surface and drifting significantly from their original habitat. Independent of the correctness of the preceding opinion, some recurring patterns have been found where the same taxa have been discovered in different regions in similar facies (Fig. 17.13 and 17.14; e.g., Westermann 1996). In such cases, one could argue that the same ammonoid taxa may have lived in the same part of a transgression or regression, which thus produced fossils in similar rock types. Especially when ammonoids are found in small basins with restricted connections to the oceans, the probability of extended distances of drift is lower. Naturally, even within small basins, a great range of habitats existed.

Ammonoids were probably not capable of long distance high speed swimming like some modern decabrachian squids or certain pelagic fishes such as tuna. For that reason, Jacobs and Chamberlain (1996) suggested that ammonoids either lived in conditions with slow currents or currents like ocean gyres or in a demersal habitat in regions with slow or absent bottom currents. In one way or the other, ammonoids had to be able to remain in a habitat with favorable conditions, i.e., sufficient food, oxygen, and also mating partners. In turn, it can be expected to find ammonoid remains more commonly in sediments typical for moderate to low water currents (Jacobs 1992b; Jacobs et al. 1994), although not in the deep sea as their shells would have imploded there, or dissolved if below the carbonate compensation depth.

There are several studies, which examined relationships between ammonoid shell shapes and sedimentary facies. For example, Batt (1989, 1993) used shell morpholo-

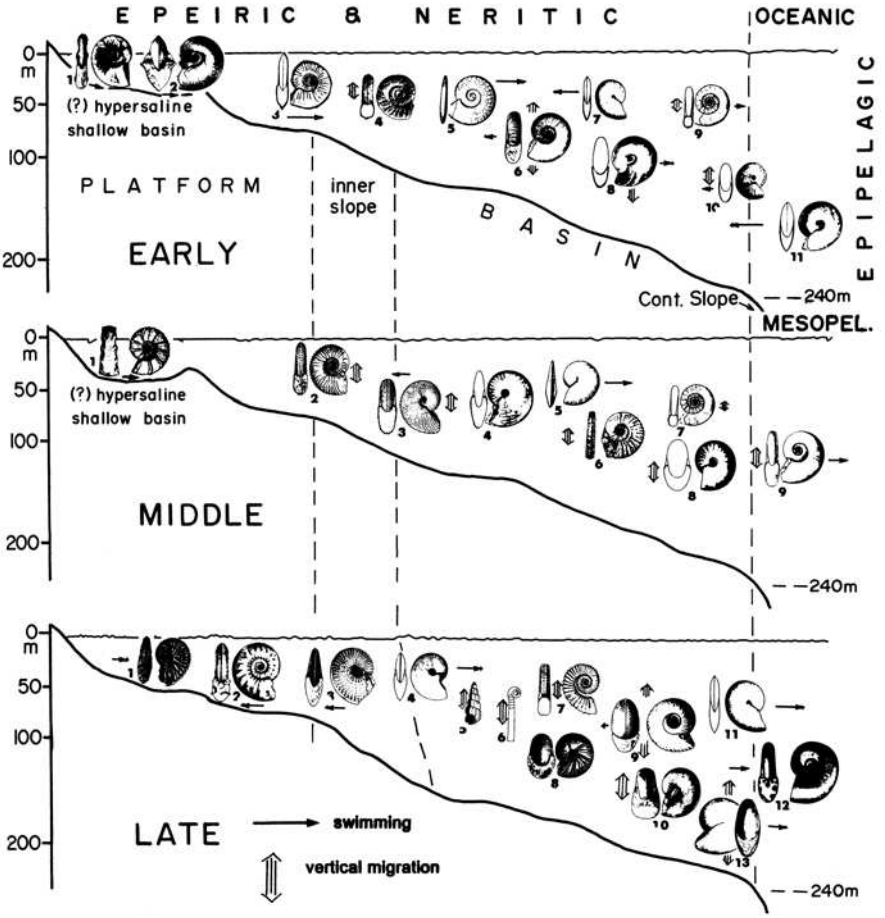

Fig. 17.13 Triassic ammonoid habitats from Wang and Westermann (1993) and Westermann (1996). Early Triassic: *1 Tirolites*, *2 Otoceras*, *3 Inyoites*, *4 Hellenites*, *5 Gyronites*, *6 Anasibirites*, *7 Hedenstroemia*, *8 Isculitoides*, *9 Leiophyllites*, *10 Paranannites*, *11 Procarnites*. Middle Triassic: *1 Ceratites*, *2 Anolcites*, *3 Trachyceras*, *4 Beyrichites*, *5 Longobardites*, *6 Balatonites*, *7 Leiophyllites*, *8 Ptychites*, *9 Monophyllites*. Late Triassic: *1 Tibetites*, *2 Distichites*, *3 Acanthinites*, *4 Discotropites*, *5 Cochloceras*, *6 Rhabdoceras*, *7 Choristoceras*, *8 Juvavites*, *9 Tropites*, *10 Cladiscites*, *11 Pinacoceras*, *12 Rhacophyllites*, *13 Arcestes*

gies to interpret oxygen availability near the sea-floor. In his opinion, heteromorphs like baculitids and loosely coiled forms lived in the water column, while the more tightly coiled heteromorphs and the normally coiled ammonoids occupied a more demersal habitat. Therefore, if the latter group is missing, this might be an indicator of hypoxic to anoxic conditions near the sea-floor (e.g., Monnet and Bucher 2007). Bayer and McGhee (1984) as well as McGhee et al. (1991) employed a more evolutionary approach. They documented how, in the parts of Middle Jurassic transgressive-regres-

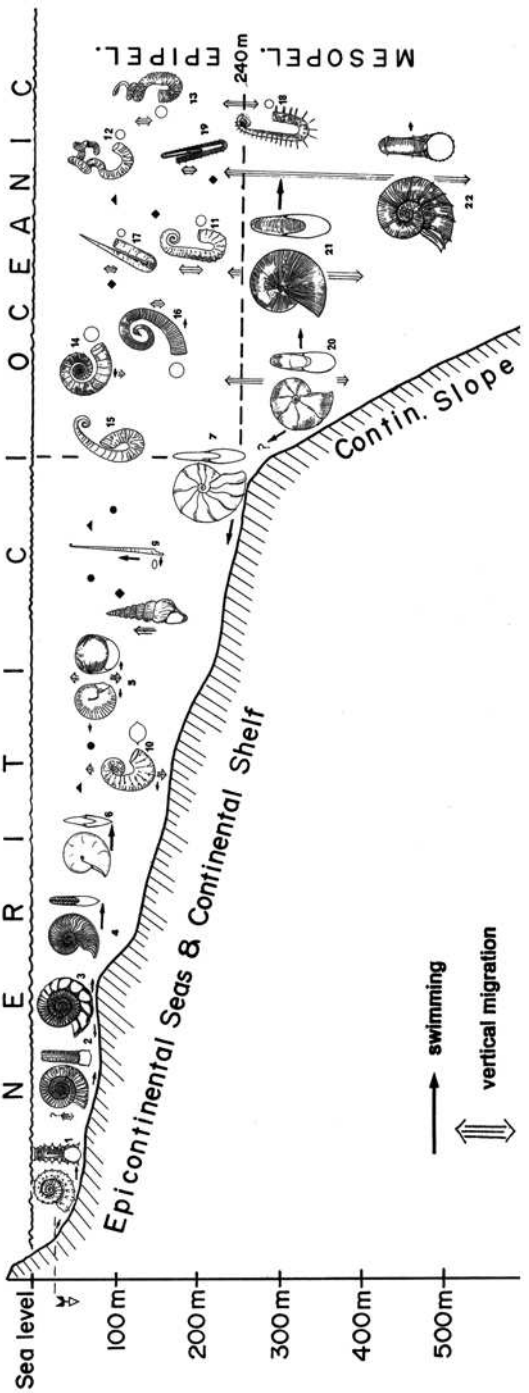

Fig. 17.14 Jurassic and Cretaceous ammonoid habitats from Westermann (1990) and Westermann (1996): *1 Peltoceras*, *2 Arietites*, *3 Perisphinctes*, *4 Harpoceras*, *5 Sphaeroceras*, *6 Oxycerites*, *7 Barremites*, *8 Turrilites*, *9 Baculites*, *10 Scaphites*, *11 Ancyloceras*, *12 Nipponites*, *13 Didymoceras*, *14 Crioceratites*, *15 Labeceras*, *16 Glyptoxoceras*, *17 Hamulina*, *18 Anisoceras 19 Pseudoxybeloceras*, *20 Holcophylloceras*, *21 Phylloceras*, *22 Lytoceras*

sive "Klüpfel cycles" with higher water energy, more involute and compressed shell forms evolved in the Leioceratinae and Graphoceratinae iteratively. Landman and Waage (1993) found that the lineages of the genera *Hoploscaphites* and *Jeletzkytes* both evolved more compressed representatives while the facies changed from the deeper water Pierre Shale to the shallower water sandy Fox Hills Formation. Jacobs et al. (1994) found that more compressed, lower drag shell morphs of *Scaphites whitfieldi* are associated with sandy facies in the Cretaceous Carlisle Shale of the American Western Interior while thicker higher drag shell morphs of the same species occur in finer grain facies. A similar pattern was reported by Courville and Thierry (1993) from *Thomasites* but inverse patterns are sometimes also found in strongly ornamented taxa such as *Schloenbachia* (Wilmsen and Mosavinia 2011), which can complicate interpretations (Ritterbush et al. 2014; De Baets et al. 2015a). Westermann (1996) listed a great number of examples for several marine basins, where he assigned certain ammonoid groups to distinct habitats (Fig. 17.13, 17.14). Klug (2002) suggested that Early and Middle Devonian anarcestids and agoniatitids, which mainly differ in whorl expansion rate and umbilical width, had different ecological preferences since he found them in more clayey or more limey facies, respectively. However, this study used low specimen numbers, thus leading to a low statistical power.

In the Early and Middle Devonian, two such lineages evolved in parallel as shown by Monnet et al. (2011). In the Auguritidae and Pinacitidae, oxyconic shell forms with closed umbilicus evolved independently, and in both lineages, the most derived forms occurred in carbonates that were probably deposited under shallower water conditions than those associated with the ancestral forms. Most of the studies listed in the preceding paragraphs appear to coincide with the interpretations of Jacobs (1992b) as well as Jacobs and Chamberlain (1996), but there are not many such studies, their statistical power tends to be low, and the causality between habit, habitat and shell morphology is difficult to establish with certainty; this can only be achieved by combining multiple lines of evidence including analysis of shell shape, facies and geographic distribution, isotope analysis, etc. (e.g., Tsujita and Westermann 1998; Ritterbush et al. 2014).

A different approach to identify habitat depth is discussed in detail in Chaps. 17.1 and 2. In these studies, stable isotopes of oxygen have been used to assess the habitat depth of various Cretaceous ammonoids (Moriya et al. 2003; Lukeneder et al. 2010). Unfortunately, the error sources of such studies are often large and the number of these studies is still too low. Examination of oxygen isotopes in ammonoid shells is still one of the most promising methods to reveal new information on ammonoid habitats.

17.7 Swimming Modes

Taking the uncertain knowledge of ammonoid soft parts into account, most interpretations of the 'ammonoid power plant' are based on actualistic comparisons. Packard et al. (1980) examined the swimming modes in Recent nautilids (see also

Crick 1898; Chamberlain 1987, 1990, 1992). In *Nautilus*, very slow movement can be produced by the water expelled through the hyponome during aeration of the gills. Normal swimming speeds are produced by mantle cavity water expelled by contraction of the cephalic retractor muscles and funnel muscles. The animal moves forward, backward, up, or down, depending on the orientation of the highly flexible hyponome (Johanson et al. 1972; Ward et al. 1977; Packard et al. 1980; Chamberlain 1981; 1987; Wells and Wells 1985; Webber and O'Dor 1986; Wells and O'Dor 1991).

Many squids including *Sepia* have lateral fins, which function in thrust production and in turning in some squid locomotor behaviors. Octobrachians and some decabrachians use their arms, sometimes connected with velar skins, to swim by expelling water entrained within their arm crowns with rhythmic beating of their arms, in the style of medusoid cnidarian bells. These two modes of locomotion appear unlikely to have been present in ammonoids, or at least, there is no evidence at all yet to support their occurrence among ammonoids.

The most likely mode of swimming is by contracting the mantle cavity, although it is not clear, which muscles were responsible for this task in ammonoids. There are several alternatives, namely the mantle musculature (as in coleoids), the cephalic retractors (as in nautilids) or potentially also other longitudinal muscles (not realized in Recent forms) in combination with the hyponome musculature. It appears also likely that the water was expelled through a hyponome, since hyponomic sinuses are present in many ammonoids. Hyponomes have not yet been found fossilized in ammonoids. Thus, another open question is the flexibility of the ammonoid hyponome. Was it long and flexible enough to point backwards and allow forward swimming?

Recently, Westermann (2013) revived a hypothesis earlier introduced by Schmidt (1930). This "*Twin nozzle-Hypothesis*" roots in the fact that many Mesozoic ammonoids have a more or less long ventral projection (e.g., in *Amaltheus*) combined with a probably more or less horizontal aperture. This would be an adverse combination of character states for straight backwards swimming, because the mentioned ventral apertural projection would have interfered with movement of the hyponome. Therefore, these authors suggested that the hyponome had evolved two openings, one on each side of the ventral projection. Both hyponome parts could be moved independently according to them. This is an interesting idea but so far, it is not supported by fossil evidence.

Monnet et al. (2011) discussed the peculiar way, in which the umbilicus was closed in some Devonian Auguritidae and Pinacitidae. The most derived representatives of both families have largely covered the umbilicus with a projection of the lateral shell over the umbilicus. This projection formed umbilical sinuses, which might have been horizontally aligned with the hyponome sinus. It would have allowed these species to take in water from the swimming direction into the mantle cavity (in *Nautilus*, water is taken in at the same place according to Packard et al. 1980), accelerating the water by compressing the mantle cavity, and expelling it out of the hyponome. This means that these forms potentially sucked water into the mantle cavity after completion of a hyponome jet.

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